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ON THE ORIGIN AND PRESENT DISTRIBUTION OF THE PINE-BARRENS OF NEW JERSEY*

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The peculiarly characteristic features of the pine-barrens of New Jersey have always attracted the interest of botanists and zoölogists. Indeed, the region is so unusual that the ordinary traveler is at once struck with the difference between these sandy plains and pine-tree vegetation, and the richer flora further north. The recent excellent flora[1] of this region by Mr. Witmer Stone has renewed interest in this botanically unique country.

The true limits of the pine-barrens are perhaps for the first time clearly drawn by Stone in this work, there having been previously considerable difference of opinion as to how far south in New Jersey the true pine-barren element extended. Formerly the pine-barrens were supposed to consist of all the remainder of the state south of their northern edge, but explorations of the botanists of Philadelphia have resulted in a final delimitation of this interesting region. The accompanying map (fig. 1) copied from Stone's book well shows the limits of the pine-barrens. The darker colored portion surrounding the white is not pine-barren in character, and maintains a very different flora from the pine-barrens.

"Some attempt has been made to correlate these areas or parts of them [the coastal plain, including the pine-barrens] with the underlying geological formation, but . . . such correlation is not

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[1] Stone, W. The plants of southern New Jersey, with especial reference to the flora of the pine-barrens. Ann. Rept. N. Jersey State Mus. 1910: 25–828. Ja 1912.

possible."[2] Notwithstanding this assertion it is the belief of the writer that not only is such correlation possible, but that, in the end, it is doubtful if there be any explanation, other than a

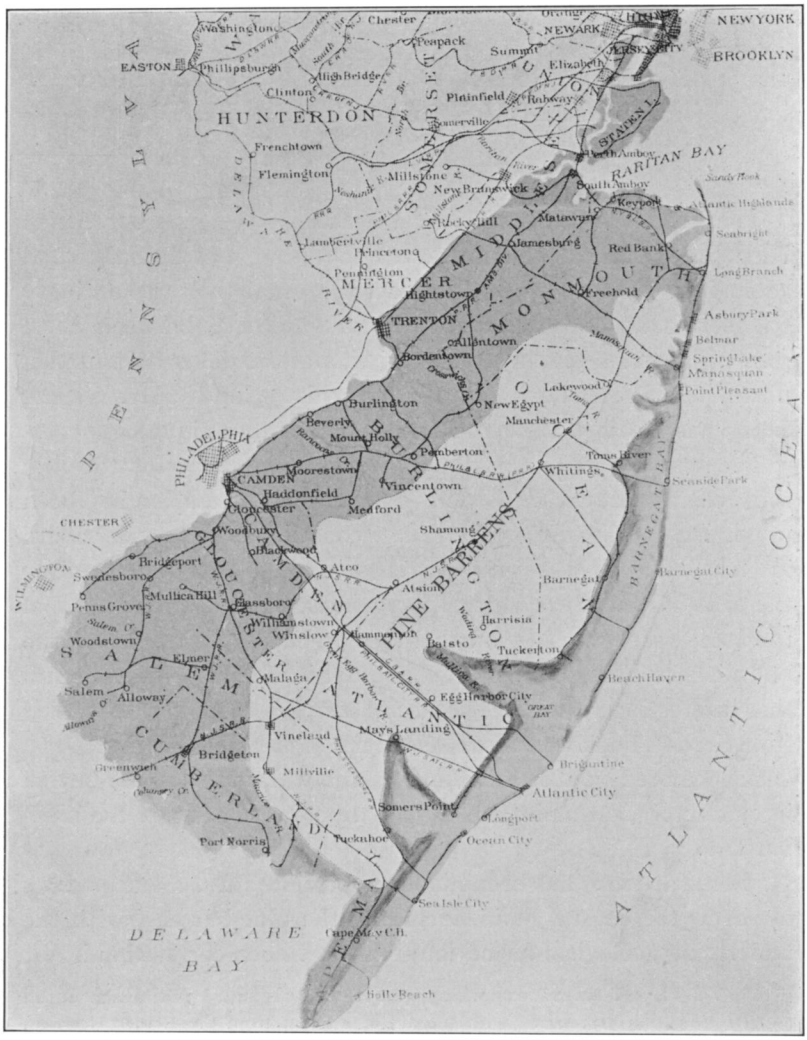

FIG. 1. Map of southern New Jersey. The unshaded area is all pine-barren; the shaded areas are not pine-barrens. Note the shaded areas along the coast and at Cape May. (From Stone's Flora.)

[2] Stone, W. *loc. cit.* 57.

geological one, that will successfully explain the peculiarly local, often endemic, nature of the pine-barrens.

Others have also sought geological explanation for the origin of this region, and one paleobotanist was the first to suggest the possibility of there being any relationship between the flora and the geology of southern New Jersey.[3] It was Hollick's suggestion that the pine-barrens are co-extensive with the Tertiary sands and gravels that Stone's work shows must be revised. Recent collections, the significance of which was, of course, unknown to Hollick in 1899, have led to the abandonment of his theory that the pine-barrens or "coniferous zone" are co-extensive with the Tertiary sands and gravels.

Much later, we find Harshberger[4] attributing the vegetation about the edges of the pine-barrens to the "post Pensauken uplift of the New Jersey geologists," which is perfectly correct. But he follows Hollick in saying that "the Tertiary soils extend southward along the Atlantic Ocean to Florida and are occupied by a pine-barren flora."[5] This, as Stone's work has shown, must be modified. But this statement of Hollick's, subsequently used in Harshberger's work, contains such a large measure of truth in relation to the origin of this unique region, that it is only to be abandoned upon presentation of a theory more nearly fitting the known facts. While the pine-barrens do occupy Tertiary soils, they do not occupy *all of them.* It is just this lack of co-extensiveness of the pine-barrens in New Jersey with the Tertiary that has led to Mr. Stone's scepticism, and to the present effort to sketch what the writer believes to have been the sequence of geological events that has resulted in the final limits of the pine-barrens.

[3] Hollick, A. The relation between forestry and geology in New Jersey. Am. Nat. **33**: 1–14, with map. 1899.

[4] Harshberger, J. W. Phytogeographic Survey of N. Am. 219. 1911.

[5] Harshberger, J. W. *loc. cit.* 218.

Geological History of the Pine-Barren Area[6]

Going back to the time when all the coastal part of New Jersey south of a line from Jersey City to Flemington (see fig. 1) was under water, owing to the last great general submergence of the continent, we find that during this period a great deal of erosion of the unsubmerged land took place. This sinking of the coastal part of New Jersey, and of course elsewhere, known to geologists as the Miocene sinking,[7] had a profound influence on the configuration of the lower part of the state. All the material from the north and northwest that was washed down, or eroded, went out with the water and was finally deposited over this submerged area, and this deposition went on for countless ages. Ultimately this Beacon Hill formation, as the geologists call the deposited material, became very thick, covering practically all the lower part of the state.

"After the deposition of the Beacon Hill formation, the area over which it had been spread was again elevated, and the history of the topography of all that part of the state, which was covered by the formation, . . . dates from this re-emergence of the surface covered by the Beacon Hill formation."[8] This emergence of the land is spoken of by geologists as the Post-Miocene uplift or Pre-Pensauken cycle of erosion. Whatever the terminology used, the result was to bring above water most of the land that had been previously submerged. Not quite all of it, however, for the land was not perfectly level, and only the highest portions came out of the water. Some of what is now the coastal strip of New Jersey, all the Cape May region and much of the lower Delaware Valley, was either not above water at all, or only slightly so, and in the latter case was soon considerably eroded. This cutting down of the emerged Beacon Hill by erosion, particularly to the south and east, was very great, so that finally it was a very different region from the great upland plain it is supposed to have been immediately after the Post-Miocene uplift.

[6] For help in criticising the geological discussion that follows, and for much previous assistance along similar lines I here gratefully express my indebtedness to Dr. Arthur Hollick.

[7] Salisbury, R. D. Geol. Survey of New Jersey 4: 92. 1892.

[8] Salisbury, R. D. *loc. cit.* 93.

This erosion of the Beacon Hill formation pictured above was brought to an end finally by the gradual subsidence of the whole region. Little by little the lower part of New Jersey sank so

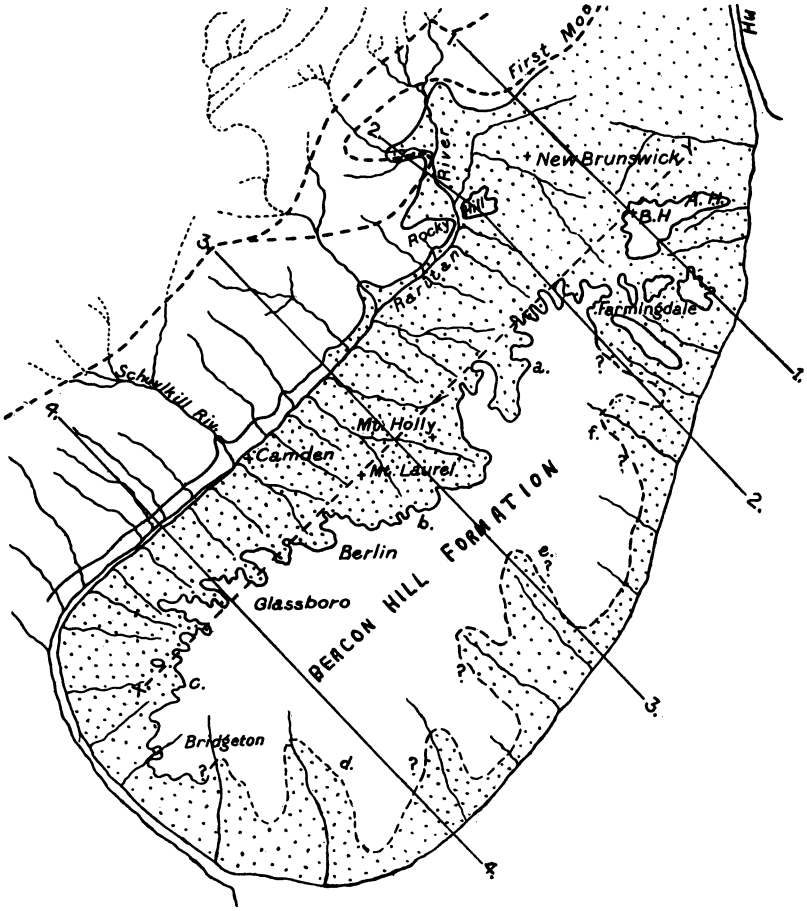

FIG. 2. Map of southern New Jersey at the time of the Pensauken Submergence. All the dotted area was under water, including the Cape May region. The undotted area has not been submerged since upper Miocene times. (*From Salisbury. Geol. Survey N. J.* 4: *pl.* 10.)

that everything but the then upland Beacon Hill formation was submerged (Pensauken Submergence).[9]

The accompanying map (fig. 2) shows the extent of the sub-

[9] Salisbury, R. D. *loc. cit.* 129.

mergence, as everything covered by the dotted area was under water. The undotted light area was not submerged, and has never since been submerged. After an indefinite period of submergence the whole dotted area was again raised so that all of lower New Jersey as we know it to-day came out of the water. The Pensauken formation, which is the geologists' name for most of the material eroded from the uninterruptedly emerged Beacon Hill, was itself subject to erosion, giving us the present characteristic stream beds of the coastal plain in the state.

The next step of serious significance was the encroachment of the ice-sheet, which came down to Perth Amboy, not more than 12–20 miles north of the Beacon Hill formation. At the final recession of the ice there is some evidence of another slight subsidence of the lower part of the state and the coastal region, but not enough to have brought the Beacon Hill formation anywhere near down to sea level. This last subsidence of the coastal strip and the Cape May region had a significant influence upon the distribution of the plants of the area. It seems very probable that a gradual sinking of this region has been going on ever since, as the sea has constantly encroached upon the land throughout maritime New Jersey, as indeed it has in Staten Island, Long Island, and further north.

Whether one follows Johnson[10] in believing that this subsidence of the coastal part of our area is not recent or continuing; or Bartlett[11] that it is both recent and continuing, does not matter so much for our present purposes.[12] Both agree, and the evidence is of such a nature that it appears incontestable, that there was a great deal of ancient subsidence. In Cape May County this has been of such an extent that whole regions covered by forests of white cedar (*Chamaecyparis thuyoides*) have been submerged, emerged, and submerged again. This, repeated several times,

[10] Johnson, D. W. Botanical evidence of coastal subsidence. Science II. 37: 721. 1910. Science II. 38: 300. 1911.

[11] Bartlett, H. H. Science II. 37: 29. 1910.

[12] The writer inclines to the views held by Mr. H. H. Bartlett in this very interesting question of coastal subsidence. Evidence of recent and progressive subsidence seems conclusive, quite apart from any question of fluctuating high tides, which seem to Dr. Johnson to be of so much importance.

has resulted in a great accumulation of buried forests. "Trunks of trees are found buried at all depths beneath the surafce, quite down to the gravel."[13] This and "numerous facts of the same kind . . . collected along the shores of the Delaware Bay and River, in Salem and Cumberland Counties, and on the sea-shore in Atlantic, Ocean, Monmouth, and Middlesex Counties,"[14] all seem to point to a decided ancient subsidence of the area surrounding the Beacon Hill formation.

For the phytogeographer the salient features of these changes are that Beacon Hill has been uninterruptedly out of the water since upper Miocene times, and that it has several times been partly, and often entirely surrounded by water. These facts, together with the encroachment of the glacier, and its recession, with the probable deposition of a great deal of morainic material around Beacon Hill, makes this formation the oldest in New Jersey, either on the coastal plain or in the glaciated regions northward, that could have been continuously covered with vegetation. This, it seems to me, is why the Beacon Hill formation is the controlling factor in the origin and present distribution of the pine-barrens. The area of the pine-barrens (see fig. 1) is not exactly coextensive with Beacon Hill (see fig. 2) but the differences are so slight that recent and local erosion of the formation would account for the failure of the two regions to superimpose, as it were.

In other words the New Jersey pine-barrens exist exclusively on this Beacon Hill formation, an area isolated by geological processes, and maintaining a relict or climax flora, the antiquity of which greatly antedates any of the rest of our vegetation hereabouts, so far as permanency of position and phytogeographical isolation are concerned. This undoubtedly accounts for the composition of the flora, and it is interesting to note that zoölogists have found this same apparent isolation, the same endemism noted above. The sphagnum frog, *Rana virgatipes*, described by Cope and collected only thrice since, is unknown outside of this region,[15] and the late John B. Smith in his work

[13] Geology of the county of Cape May 62. 1857.

[14] *Ibid.* 39.

[15] Fowler, H. W. Proc. Acad. Nat. Sci. Philadelphia **57**: 662–664. 1905.

on the insects of New Jersey has figured the "entomological pine-barrens" as very nearly coinciding with the floral pine-barrens.[16] I have not been able to find any explanation of these curious distributional features, by a zoölogist; but it would seem that perhaps the outline given above may also explain for them the endemism of the pine-barrens.

In the light of this historical outline it should be easy to trace the development of the pine-barren vegetation from the Miocene uplift until the present. Ancestrally it must have consisted of purely American plants, and most of these, in all probability, were of southern extraction.[17] Of the 565 species reported growing in the region, not counting weeds, 386 are listed as truly pine-barren. This does not mean that they are found nowhere else, but that so far as New Jersey is concerned these plants find their greatest development in the pine-barrens. There is a small element among them practically unknown outside of the pine-barrens of New Jersey, such as *Abama americana*, *Sporobolus Torreyanus*, *Eupatorium resinosum*,[18] *Chrysopsis falcata*, and *Juncus caesariensis*.[18] Besides these there are 12 species found predominately in this region, whose distribution is restricted from Massachusetts on the north to Delaware on the south, and whose undoubted distribution-centers are the pine-barrens.

It would seem likely that the 386 pine-barren species mentioned above which are now found elsewhere on the coastal plain have spread there since the release of the Beacon Hill formation from its last isolation. Perhaps future studies may be able to show, even in the pine-barrens themselves, a greater development of the typically endemic pine-barrens in the interior, than is found near the edges where the former and existing tension between other elements has left greater evidences.

At the advance of the ice there must have been a great invasion of northern species, many of which are still found in the pine-

[16] Ann. Rept. N. Jersey State Mus. 1909. Map (frontispiece). 1910.

[17] Over 180 species of the *present* flora range from Virginia to Florida and northward. Of these more than 70 find their northernmost limits in the pine-barrens. The others are found further north, into Massachusetts and Rhode Island. These and subsequent figures are from Mr. Stone's excellent tabulations.

[18] Apparently unknown elsewhere in the world.

barrens. If, as seems probable, no very great refrigeration took place in the area under consideration[19] it is within the realm of probability that the pine-barren vegetation existing then on the Beacon Hill formation, was not very seriously disturbed climatically. We have geological evidence that it was never subjected to any deposition of glacial material or over-wash; it contains no glacial terraces, for its elevation, perhaps greater then than now, precluded this. But the region surrounding Beacon Hill was in no such fortunate position. Having only recently emerged, comparatively, and boasting only a meager altitude it was more or less overrun with the material from the ice. The glacial terraces of the lower Delaware, the nature of the material deposited near Cape May and in Cumberland County all point to a local, or perhaps wide-spread subsidence of the region, which, however, did not affect the Beacon Hill formation as far as possible glacial influence is concerned. Furthermore, there is evidence in the sunken forests at Cape May mentioned above, and in the character of the present vegetation,[20] of the effects of the encroachment of glacial material from the north, by way of the Delaware Valley.

If the ice did not affect the pine-barrens geologically so much as it did the surrounding country, there seems little doubt that it was at this time that many additions were made to the flora of that region. All the following species, ranging as they do from the far north to the pine-barrens of New Jersey,[21] show unmistakable evidences of having come down with the glacier,

[19] This is a conclusion warranted by our knowledge of modern glaciers. While the refrigeration must be very great near the source of glaciers it is a well known fact that at the edges, refrigeration diminishes greatly, particularly where the ice is thin, as it was in all probability near the moraine in New Jersey. It is a common characteristic of glaciers that plants are found almost up to the edge of the ice and sometimes on it. See Muhlenbergia 7: 103, 111, 121. 1912.

[20] Mr. Stone has collected many plants at Cape May unknown in the pine-barrens, and some not known elsewhere south of the "fall line." The present distribution of *Tsuga canadensis* in New Jersey is also probably attributable to the factors noted above. It is common along the drainage of the Delaware River in lower New Jersey (the region of glacial terraces) but unknown in the pine-barrens. It is, of course, common northward. See Stone, *loc. cit.* 93.

[21] Some are now found elsewhere in New Jersey, but, as I have shown above, probably because of their subsequent migration from Beacon Hill.

and of having become isolated in bogs and other edaphically favorable locations, such as probably were only to be found on Beacon Hill at that time: *Triglochin palustris*, *Panicularia obtusa*, *Scirpus subterminalis*, *Carex livida*, *C. exilis*, *Utricularia intermedia* and *Aster nemoralis*. There are a good many more,[22] and the same phenomenon has been noted by entomologists. Prof. Smith writes of *Trechus chalybeus*, and a few other insects, that "the only trace of real boreal species has been found in the deep cold swamps of Ocean County."[23]

In this connection the distribution of the most remarkable plant of the pine-barrens, *Schizaea pusilla* is very interesting. It is found only in the pine-barrens and in Nova Scotia and Newfoundland, and is unknown between these points. If Dr. Scharff's recently proposed theory[24] that perhaps parts of Nova Scotia and Newfoundland remained unglaciated through all the period of the Pleistocene is correct, then it is not impossible that *Schizaea* is a relict in the pine-barrens of its southern migration, and that it is also a relict in the north, all the intervening territory having been preëmpted first by the ice, secondarily by more "agressive" plants after the recession of the ice. This is little more than interesting speculation, but Scharff, whether wrong or right in his contention, has opened up a wide field of discussion. It is certainly significant that *Schizaea* is not found in the unquestionably glaciated country, and is found only in the pine-barrens and in the [probably] unglaciated northeast.

Another feature of the pine-barrens which may support the theory that they are a very ancient and isolated phytogeographical entity is the number of parasitic, saprophytic and mycosymbiotic plants that grow there. Cowles,[25] in his recent treatment of those plants not wholly dependent on their own roots for food, has made the suggestion that the origin of the parasitic, saprophytic, and mycosymbiotic habit may have

[22] Stone, W. *loc. cit.* 49, 50, and 76.

[23] Ann. Rept. N. Jersey State Mus. **1909**: 30. 1910.

[24] Scharff, R. F. Distribution and origin of life in North America. New York. 1912. For further data on this point see also Adams, C. C. The Post-glacial dispersal of the North American Biota. Rept. Int. Geog. Cong. **8**: 623–637. 1904.

[25] Coulter, J. M., Barnes, C. R., and Cowles, H. C. Text-book of Botany. **2**: Ecology, 775 and 799. 1911.

been mere chance at first, then increased perhaps by the greater ease of one species as against its neighbors in getting its food, or to the failure to get food without some such reciprocal relation. The inference that this non-autophytic habit is due to isolation and consequent necessity of seeking other than "regular" methods of getting food, in a region, perhaps ancestrally offering an inaccessible food supply, may not be without significance. It is certainly of interest in this connection to note the well known high percentage of monocotyledons,[26] Pinaceae, Fagaceae, Scrophulariaceae, and Ericales, all of which are mostly non-autophytic.[27] So far as Orchidaceae and some of the monocotyledonous families are concerned the number of *species* is disproportionately large as compared with the surrounding country. Among some families, Fagaceae, Pinaceae and Ericaceae for instance, it is the number of *individuals* that is so great, forming practically exclusive growths in the case of *Pinus rigida* and *Chamaecyparis thuyoides*. This very general prevalence of the non-autophytic habit may have had something to do with the failure of many wholly autophytic plants, surrounding the Beacon Hill formation, to gain a foothold there, for the mutual exclusiveness of the diverse habits is obvious. There may, however, have been quite other factors operative here than antiquity and isolation. It would be interesting in this connection to compare the flora of the pine-barrens with some other region of similar geological antiquity. The driftless area of Wisconsin seems, at first thought, to be similarly conditioned geologically, but there is evidence that it could not have been steadily vegetated during the Pleistocene, as it was covered by water during some part of this period.[28]

The extra-territorial distribution of some of the typical pine-

[26] Stone, W. *loc. cit.* 75. See also Harper, R. M. Torreya **12**: 224. 1912. Torreya **5**: 207–210. 1905.

[27] According to E. Stal (Der Sinn der Mycorhizenbildung, in Jahrb. Wiss. Bot. **34**: 539–668. 1900) in the following families many, if not all the species, are mychorhizal, Orchidaceae, Amaryllidaceae, Liliaceae, Caryophyllaceae, Saxifragaceae, Fagaceae, Papilionaceae, Gentianaceae, Ericaceae, Scrophulariaceae and Coniferae. There are many other individual cases.

[28] Chamberlain, T. C., and Salisbury, R. D. Driftless area of the Upper Mississippi Valley. Ann. Rept. U. S. Geol. Sur. **6**: 199–322. 1885.

barren flora contributes some data that support the views outlined above. Particularly the finding of *Xerophyllum*, *Helonias*, and *Oceanorus*, to mention only a few, on the mountains of eastern Tennessee, is of interest. These and many more were found by Kearney[29] and more recently by Small, in geologically the most ancient area in America (Archaean). The hiatus in the distribution of these plants between the pine-barrens and these very old mountains is easily explainable by the isolation theory above advocated. The fact that they are wanting or very rare in the intervening territory would seem to present strong evidence of the unavailableness of this intermediary area (most of it was under water), during the geological changes described above, for the perpetuation of the species now so far isolated. Furthermore this southern isolation strongly favors the statement made above that most of the pine-barren flora was of southern extraction, for it is quite reasonable that the species found on the Tennessee mountains and in the pine-barrens of New Jersey are simply relicts of an ancient American southern flora that must, at one time, have covered a vastly greater area than it does to-day. The present nearly complete isolation and the post-glacial distribution of this southern flora, both it seems to me, favor this view.

There remains still to be considered the "pine-barren" plants of Long Island and Staten Island, not to mention regions further east. As Stone has shown a good many of these alleged "pine-barren" plants are only coastal plain plants,[30] which are found, it is true, in the pine-barrens; but more commonly in the area surrounding them, frequently throughout the Atlantic seaboard from Massachusetts to Florida. It should be remembered in this connection that neither Long Island nor Staten Island are in the same geological category as Beacon Hill. For both the former were in part covered by the glacier and both were more or less within the influence of glacial activity.[31] It is, of course,

[29] The pine-barren flora in the East-Tennessee Mountains. Plant World 1: 33–35. 1897.

[30] Stone, W. *loc. cit.* 73.

[31] Long Island was not covered wholly by glacial drift, but the sandy plain south of the moraine received considerable overwash material, now mixed with the underlying Tertiary sand and gravel.

a matter of pure speculation whether any vegetation persisted during the Pleistocene on Long Island or not, but evidence seems to point to the negative probability. If this is true then all of the New Jersey flora now found on Long Island must have had a post glacial origin. The distribution of *Pinus echinata*, *P. virginiana* and the red squirrel may throw some light on the post-glacial chronology of events on Lond Island. Both these pines are found in the region surrounding the pine-barrens, but are unknown, or very rare in them. *Pinus rigida* the predominant tree of the barrens is common on Long Island, but the two pines mentioned above and the red squirrel are not known on the island.[32] From the geological outline given above we know that *P. virginiana* and *P. echinata* must have occupied the region surrounding the pine-barrens long after the last effects of the ice were past. This may also have been true of the red squirrel. At any rate, after a large post-glacial migration of alleged "pine-barren" plants, the avenue of migration must have been broken. The discontinuance of this passageway must, it seems to me, have been the controlling factor in the failure of *Pinus echinata*, *P. virginiana* and the red squirrel to reach Long Island. It is curious in this connection that both the pines, but not the animal, are found on Staten Island. The geological events causing this very decided cut-off are outside the scope of this paper. It may, however, have been something other than geological phenomena operating here. There are, of course, many more species than these pines, which apparently reach their northern distribution point in the region surrounding Beacon Hill, or in Staten Island, never having been reported from Long Island. It seems probable that they came northward in post glacial times, too late to avail themselves of the already destroyed avenue of migration.

One other extra-territorial occurrence of pine-barren species should be noted. A widely quoted paper of Britton's[33] is often cited in support of the theory that pine-barren plants are not

[32] The reported occurrence of *Pinus virginiana* in Suffolk Co., L.I., by Miller and Young cannot be verified. It was probably a misdetermination of *P. rigida*.

[33] Britton, N. L. On the existence of a peculiar flora on the Kittatinny mountains of northwestern New Jersey. Bull. Torrey Club 11: 126–128. 1884.

strictly confined to their supposed home, and that their occurrence in edaphically favorable places in the Kittatinny mountains was an example of such phytogeographical instability. A careful reading of Dr. Britton's paper shows that not only did he make no such claim, but that all the plants mentioned there, with one exception, are not pine-barren plants, strictly speaking, at all. They are all merely plants of the sandy coastal plain, *Corema Conradii*, a true pine-barren plant, being the one exception. The distribution of this species and of the many others now found isolated outside of the pine-barrens, is to be sought in the post-glacial history of the region to the north. In the general vegetative scramble, so to speak, to cover the country uncovered by the retreating ice, it seems natural that those plants whose ancestral home had been in sand, should "choose" sand as a stopping place. It would, in reality, be strange if they had done anything else, and it is significant that all the plants mentioned by Britton are sand plants.

All of these evidences,—the geological history of the country, the isolation of Beacon Hill and the consequent isolation of the ancient pine-barren flora upon it, the post-glacial migration of some of the pine-barren species, and finally the present distribution of the pine-barrens, coinciding as it does so closely with the Beacon Hill formation, seem incontestably to point to a geological explanation of the origin and present distribution of the pine-barrens. Such a conception of the origin of this phytogeographical region entails a readjustment of our ideas as to the relative age of the flora and of some related phenomena; for, if this theory is correct, then the pine-barrens can no more be considered as a new or pioneer vegetation, but rather as an old and climax condition, ancestrally infinitely more ancient than anything in the surrounding area.

Brooklyn Botanic Garden